- HANAWALT, F. A. (1922): Habits of the common mole *Scalopus aquaticus machrinus* (Rafinesque). Ohio J. Sci. 22, 164–169.
- HARRIS, Č. E.; PETERSEN, M. K. (1979): Comparative swimming performances in selected cricetid and heteromyid rodents. Occas. Pap. Zool. 3, 1–16.
- HICKMAN, G. C. (1977): Swimming behavior in representative species of the three genera of North American geomyids. Southwest. Nat. 21, 531–538.
- HICKMAN, G. C. (1978): Reactions of Cryptomys hottentotus to water (Rodentia: Bathyergidae). Zoologica Africana 13, 319–328.
- HICKMAN, G. C. (1979): The mammalian tail: a review of functions. Mammal Rev. 9, 143-157.
- HICKMAN, G. C. (1982): Climbing ability of the star-nosed mole, Condylura cristata (Talpidae). Säugetierkdl. Mitt. 40, 296-297.
- HICKMAN, G. C. (1983a): Burrows, surface movement, and swimming of *Tachyoryctes splendens* (Rodentia: Rhizomyidae) during flood conditions in Kenya. J. Zool., London, 200, 71-82.
- HICKMAN, G. C. (1983b): Swimming ability of a naked mole-rat (*Heterocephalus glaber*). Mammalia 47, 267–269.
- HICKMAN, G. C. (1984a): Influence of the semi-aquatic habit in determining burrow structure of the star-nosed mole (Condylura cristata). Canadian J. Zool. 61, 1688–1692.
- HICKMAN, G. C. (1984b): Swimming ability of talpid moles with particular reference to the semiaquatic Condylura cristata. Mammalia 48, 505-513.
- HICKMAN, G. C. (1984c): Behavior of North American geomyids during surface movement and construction of earth mounds. Special Publ. Mus. Texas Tech. Univ. 22, 165–186.
- HICKMAN, G. C. (1985): Surface-mound formation by *Ctenomys fulvus* (Rodentia: Ctenomyidae) with comments on earth-pushing in other fossorial mammals. J. Zool., London, 205, 385-390.
- HICKMAN, G. C. (1986): Swimming of Amblysomus hottentotus (Insectivora: Chrysochloridae) with notes on Chrysospalax and Eremitalpa. Cimbabesia, (A) 8, 55-61.
- HICKMAN, G. C.; MACHINE, C. (1987): Swimming behaviour in six species of South African rodents (Cricetidae, Muridae). Acta Theriologica 31, 447–464.
- HICKMAN, G. C.; NEVO, E.; HETH, G. (1983): Geographic variation in the swimming ability of Spalax ehrenbergi in Israel. J. Biogeogr. 10, 29–36.
- Howell, A. B. (1930): Aquatic mammals their adaptations to life in water. Baltimore: Charles C. Thomas.
- HUEY, L. M. (1941): Mammalian invasion via the highway. J. Mammalogy 22, 383-386.
- KENNERLY, T. E., JR. (1963): Gene flow and swimming ability in the pocket gopher. Southwest. Nat. 8, 85–88.
- KING, J. A. (1961): Swimming and reaction to electric shock in two subspecies of doormice, *Peromyscus maniculatus*, during development. Anim. Behav. 9, 142–150.
- McCulley, H. (1967): The broad-handed mole, *Scapanus latimanus*, in a marine littoral environment. J. Mammalogy 48, 480–482.
- MERRIAM, C. H. (1884): The star-nosed mole amphibious. Science 4, 429.
- MILLER, M. A. (1957): Burrows of the Sacramental Valley pocket gopher in flood-irrigated alfalfa fields. Hilgardia 26, 431-452.
- MOORE, A. W. (1939): Notes on the Townsend Mole. J. Mammalogy 20, 499-501.
- NEVO, E. (1979): Adaptive convergence and divergence of subterranean mammals. Ann. Rev. Ecol. Syst. 10, 269–308.
- PINE, R. H. (1975): Star-nosed mole eaten by bullfrog. Mammalia 39, 713-714.
- REED, C. A.; RINEY, T. (1943): Swimming, feeding, and locomotion of a captive mole. Amer. Midl. Natur. 39, 790–791.
- SAVAGE, I. R. (1973): A stream as a barrier to homing in *Peromyscus leucopus*. J. Mammalogy 54, 982–984.
- SCHAPIRO, S. M.; SALAS, M.; VUKOVITCH, K. (1970): Hormonal effects on ontogeny of swimming ability in the rat: assessment of the central nervous system development. Science 168, 147–151.
- SCHMIDLY, D. J.; PACKARD, R. L. (1967): Swimming ability in pocket mice. Southwest. Nat. 12, 469-487.
- SMITH, M. F.; PATTON, J. L. (1980): Relationships of pocket gopher (*Thomomys bottae*) populations of the lower Colorado River. J. Mammalogy 61, 681–696.
- STARRET, A.; FISHER, G. F. (1970): Aquatic adaptations of the water-mouse, *Rheomys underwoodi*. Contrib. Sci. (Los Ang.) 182, 1-4.
- STOCK, A. D. (1972): Swimming ability in kangaroo rats. Southwest. Nat. 17, 98-99.
- VLECK, D. (1979): The energy cost of burrowing by the pocket gopher *Thomomys bottae*. Physiol. Zool. 52, 122–136.
- WALKER, E. P. (1975): Mammals of the World. Baltimore: John Hopkins Univ. Press.
- WILBER, C. G. (1958): Biological similarity and swimming time in rodents. Anat. Rec. 131, 608–609.
 WILBER, C. G. (1959): Some factors which are correlated with swimming capacity in guinea pigs. J. Appl. Physiol. 14, 199–203.
- WILBER, C. G. (1963): The swimming capacity of the golden hamster. J. Mammalogy 44, 265-267.

- 169-175.
- WILBER, C. G.; WEIDENBACHER, G. H. (1961): Swimming capacity of some wild mammals. J. Mammalogy 42, 428-429.

Author's address: Dr. GRAHAM C. HICKMAN, Department of Zoology and Entomology, University of Natal, P.O. Box 375, Pietermaritzburg, 3200 Natal, R.S.A.

Wild boar social groupings and their seasonal changes in the Camargue, southern France

By Maryse Dardaillon

Centre de Recherches en Biologie du Comportement, Toulouse, France

Receipt of Ms. 29. 1. 1987

Abstract

Wild boar social organization and its monthly changes were studied from 872 sightings of groups, recorded in the Camargue (southern France) from December 1975 through February 1983. Groups, comprised of 1 to 23 animals, were classified according to their composition. There were three recognized age categories: piglets, subadults, and adults. Of the 872 groups, 240 (27.5 %) were single adults, 134 (15.4 %) consisted of adults grouped together and 119 (13.6 %) were subadults observed either singly or grouped together. The most frequent groups (N = 379, 43.5 %) were matriarchal units; they were generally comprised of 1 to 5 sows with their piglets and/or yearlings. The study of monthly variations in the percentage frequency observed for the various group categories showed that the social structure of wild boar is a dynamic system that changes throughout the year in relation to the farrowing and breeding seasons.

Introduction

Despite the large literature on wild pigs (MAUGET et al. 1984), there is little information on their grouping patterns.

Group size and composition have been described in some studies dealing with the general ecology and behaviour of the species (SLUDSKII 1956; SNETHLAGE 1957; GUND-LACH 1968; EISENBERG and LOCKHARDT 1972; FRÄDRICH 1974; BEUERLE 1975; GRAVES and GRAVES 1977; BARRETT 1978; SHAFFER 1979; SANTIAPILLAI and CHAMBERS 1980; SINGER and ACKERMAN 1981; MEYNHARDT 1982). Formation of family units appears characteristic of wild pigs. Their social organization has been described as a matriarchal society with the basic family group comprised of a sow and its young of the year. Multifamily groups, composed of several sows with their young have been termed "sounders" by EISENBERG and LOCKHARDT (1972). Extended family groups also include subadults which are presumably offspring of the previous year (SHAFFER 1979). In contrast, adult males are solitary; they join females only during the breeding season.

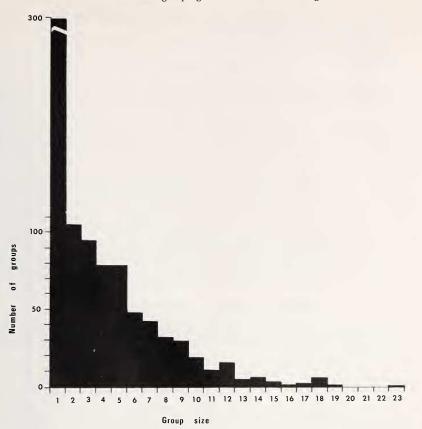
Little attention has so far been paid to seasonal changes in grouping patterns and their determining factors. SLUDSKII (1956) or SANTIAPILLAI and CHAMBERS (1980) have shown that various environmental factors such as temperature, snow cover or availability of food can cause changes in group size of wild pigs. In other respects, various results indicate that changes in social organization occur during rutting and farrowing time.

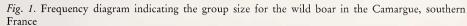
The present paper reports a study of group size and composition of wild boars living in the Camargue, and analyzes changes related to the farrowing and breeding seasons.

Study area

Sightings of wild boar groups have been recorded at the Tour du Valat Reserve, which is privately owned land with minimal human access. It covers an area of 1500 ha and is located in the southeastern part of the Rhône delta. Lying to the east of the Camargue National Reserve, the area is surrounded on its other sides either by cultivated land or by more or less natural ground.

U.S. Copyright Clearance Center Code Statement: 0044-3468/88/5301-0022 \$ 02.50/0





Material and methods

Observations and sightings of wild boar groups were mainly made by game wardens and researchers of the "Tour du Valat Biological Station" during their regular field work. From December 1975 through February 1983, these observers noted the composition and location of the wild boar groups observed on pre-established tables and maps, which were fixed on a board in the hall of the research building.

The animals observed were classed in three age categories according both to their estimated weight and coat color. Piglets, i.e. young with a striped coat, were generally less than 4 months old and weighed less than 15–20 kg. Subadults had a reddish or black coat, and a weight varying from 15–20 to 30–40 kg. Adults referred to animals more than 2 years old; they looked big, heavy and dark or silver grey colored.

With a few exceptions, sex was not specified because it could not be reliably determined at a distance.

Results

A total of 3530 animals in 872 distinct sightings were observed during the 7 years of the study. Of the 3530 wild boars observed (fig. 1), 240 (8.2 %) were single adults, 59 (1.7 %) were single subadults or piglets, while 3241 (91.8 %) animals were encountered in 583 groups composed of 2 through 23 animals. The most frequent group sizes were 2 (18.0 %)

and 3 (16.3 %), then 4 and 5 (13.5 % each). Groups of more than 10 animals were seen only occasionally (12.3 % of the 583 groups).

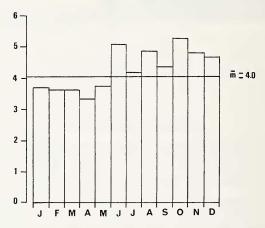
Group categories

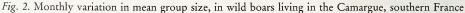
The 872 sightings ranged in the 11 following categories: 1. Single adults (n = 240, 27.6 %); 2. Adult-groups (n = 134, 15.4 %); 3. Single subadults (n = 41, 4.7 %); 4. Subadultgroups (n = 78, 8.9 %); 5. Groups of both adults and subadults (n = 281, 32.2 %); 6. Basic family group = 1 adult with piglets (n = 27, 3.1 %); 7. Sounders = several adults (2 to 5) with piglets (n = 36, 4.1 %); 8. Extended family groups = adults with both piglets and subadults (n = 16, 1.8 %); 9. Single piglets (n = 8, 1.0 %); 10. Piglet-groups (n = 9, 1.0 %); 11. Subadult- and piglet-groups (n = 2, 0.2 %).

Categories numbered 5 to 11 must all be considered as matriarchal in nature. Groups of adults with piglets include the categories "family groups" (n° 6) and "sounders" (n° 7), previously mentioned, whereas groups comprised of adults and subadults (n° 5) are supposedly a later stage of this type of association. Category n° 8 has previously been termed "extended family group". The 19 groups that make up the categories n° 9, 10 and 11 have to be included in matriarchal associations because they all had at least one piglet; we suppose that one or more sows were either absent or out of sight for the observer.

Monthly variation in average group size

The average group size was about 4 animals. It ranged from 3.3 to 3.7 from January to May. It exceeded the annual average from June through December, ranging from 4.2 in July to 5.2 in October (fig. 2).





A more precise analysis has revealed that the proportion of groups formed of at least 4 animals increased from July through December, whereas that of groups including less than 3 animals decreased. The shift is observed only in August if the comparison takes into account groups of more than 5 animals and those of less than 4 animals. This means that wild boars regroup gradually during the summer and autumn seasons, and consequently live in larger groups during the second part of the year than during the first part.

Table. Monthly changes in the relative frequency of the various wild boar group categories observed in the Camargue (southern France)

n° Group category	ŗ	щ	W	Α	M	Ĺ	ŗ	Α	S	0	N	D	Total
1 Single adults	40	34	44 21 7	31 30 0	16	5 23 0	7	7	6	20	15	12	240
2 Adult-groups	21.22	22 22	21./ 19	29.0 14	0.12 6	6.07 4		18.U	40.4 5	24.4 15	21.4 13	c.c2	c./2 134
0	17.8	18.8	13.7	13.5	10.3	19.0		7.7	11.3	18.3	18.6	17.7	15.4
3 Single subadults	9	9	3	13	2	0		3	1	ę	7	0	41
)	5.1	5.1	2.2	12.5	3.5	I		7.7	2.3	3.7	2.9	I	4.7
4 Subadult-groups	6	7	14	14	6	Э		1	4	5	5	5	78
•	7.6	6.0	10.1	13.5	15.5	14.3		2.6	9.1	6.1	7.1	9.8	8.9
5 Adults with	38	44	54	10	1	1		18	20	36	33	22	281
subadults	32.2	37.6	38.8	9.6	1.7	4.8		46.1	45.4	43.9	47.1	43.1	32.2
6 Basic family	1	1	1	6	ŝ	0		0	1	1	0	ŝ	27
groups	0.9	0.9	0.7	8.7	8.6	I		I	2.3	1.2	I	5.9	3.1
7 Sounders	ĉ	2	2	6	10	e,		7	0	0	2	0	36
	2.5	1.7	1.4	8.7	17.3	14.3		5.1	I	I	2.9	I	4.1
8 Extended family	0	1	1	2	ę	4		0	1	2	0	0	16
groups	I	0.9	0.7	1.9	5.2	19.0		I	2.3	2.4	I	I	1.8
9 Šingle piglets	0	0	1	0	1	1		ę	1	0	0	0	8
2	I	I	0.7	I	1.7	4.8		7.7	2.3	I	I	I	0.9
10 Piglet-groups	0	0	0	2	4	0		2	1	0	0	0	6
	I	I	I	1.9	6.9	I		5.1	2.3	I	I	I	1.0
11 Subadults with	0	0	0	0	1	0		0	1	0	0	0	2
piglets	I	1	I	I	1.7	I		I	2.3	I	I	I	0.3
Subtotal	4	4	5	22	24	8	11	7	5	3	2	. 3	86
categories 6 to 11	3.4	3.5	3.5	21.2	41.4	38.1	37.9	17.9	11.5	3.6	2.9	5.9	, 11.2
Total	118	117	139	104	58	21	29	39	44	82	70	51	872

Maryse Dardaillon

Monthly changes in group composition

Changes concerning groups with piglets

98 groups – categories n° 6 to 11 – included at least one piglet (table). Their percentage frequency greatly increased in April (fig. 3) and reached its maximum in May (41.4 %, table) when most females had given birth; at that time piglets follow their dam and were thus more easily sighted.

Piglets were seen alone in 11.1 %, 16.3 % and 58.3 % of the observations in March-April, May through June and August-September,

respectively. This result indicates that as they increase in age piglets spend relatively less time in the close vicinity of their dam.

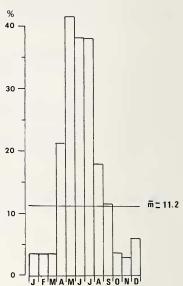
Groups including piglets became rarer in August, then again in September when piglets changed their coat color and were therefore identified as subadults by the observers (fig. 3).

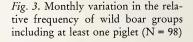
From October through March, the monthly frequency was low and more or less constant. A basic level, less than 5–6 % (table), was registered during this period, which means some births occurred every month.

The maximal percentage frequency of basic family groups was observed in April and May (fig. 4^{F}), whereas that of sounders and extended family groups was reached in May for the first category (fig. 4^{G}) and in June for the second (fig. 4^{H}).

Changes concerning subadults

The percentage frequency of groups comprised of both adults and subadults greatly diminished in April (-29.2 %, table). At the same time, sightings of single subadults and of subadult-groups increased





respectively from 2.2 to 12.5 % and from 10.1 to 13.5 % (table). These variations are related to changes in social organization which happen during the prefarrowing period. At that time, sows become separated from their congeners and thus from subadults.

Single subadults were most frequently observed in April (fig. 4^{D}). They certainly regrouped during the following weeks as indicated by comparison of figures 4^{D} and 4^{E} . We can thus observe that the percentage frequency of single subadults diminished in May and June, whereas that of subadult-groups became higher than in April.

Groups comprised of females with both piglets and subadults were formed again during May through July (fig. 4^{H}). We therefore observed that the frequency of subadult-groups clearly decreased from May through August (fig. 4^{E}) whereas groups of adults with subadults (fig. 4^{C}) increased by 44.4 %. The increase was particularly high (+32.4 %, table) between July and August because piglets, which had lost their stripes, were subsequently identified as subadults by the observers.

Changes concerning adults

Sightings of adults observed either alone or grouped together (fig. 4^{A,B}) decreased progressively from April through August (respectively -11.8 % and -5.8%, table), on

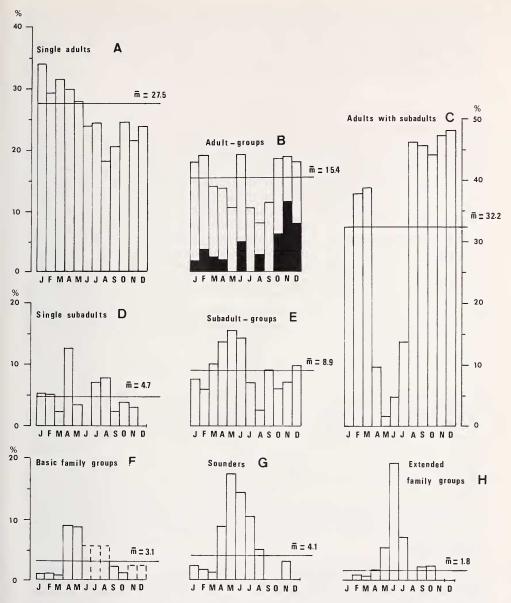


Fig. 4. Monthly variation in the relative frequency of the various group categories, in wild boars living in the Camargue, southern France. In the fig. 4^B black parts indicate relative frequency for adult-groups comprised of at least 5 animals

account first of the birth of piglets then of the reformation of extended family groups. From August through March, adults were encountered mainly in the company of subadults (table). However, adult-groups were rather frequent from October through February (fig. 4^{B}). Adults appeared to regroup in September (+3.6 %) then in October (+7.0 %). The percentage frequency of groups including at least 5 adults was clearly above the average annual percentage from October through December (fig. 4^{B}). This regrouping

Maryse Dardaillon

of adults was related to the onset of the breeding season which was at its peak in early December. Afterwards, some adults, especially male wild boars, became solitary again as attested by the increase (+10.4 %, table) in the percentage frequency of single adults in January (fig. 4^{A}). At that time, adult-groups remained rather frequent (fig. 4^{B}), but they were smaller than observed during the prerut and rut seasons.

Discussion

Wild boars living in the Camargue exhibit the same basic social organization as has been previously described in other areas. Adults live either singly or in groups almost always including juveniles (subadults and/or piglets). According to the literature and our own observations of marked individuals (unpublished data), we think that single wild boars are mainly males whereas those living in groups are sows. When not in the company of adults, subadults are encountered either alone or grouped together.

Our results show that the social structure of wild boar is a dynamic system that changes throughout the year in relation to the farrowing and breeding seasons. At farrowing time, i.e. mainly in April, matriarchal groups are disrupted when gestating sows become isolated some days before they give birth. MEYNHARDT (1982) observed a 4-year female at farrowing time and reported that the female was followed by its young of the previous year when separating from congeners; afterwards, young remained with their mother which kept them at a distance of at least 20 m during nest building, farrowing and the postpartum period. However, the separation from congeners seems to be the rule in most other areas (SNETHLAGE 1957; GUNDLACH 1968; FRÄDRICH 1974). In addition, a number of radiotracking studies have shown that sows reduce their movements and tend to center their activities around nests before farrowing (KURZ and MARCHINTON 1972; BARRETT 1978; MAUGET 1980; DOUAUD 1983; JANEAU and SPITZ 1984). Consequently, subadults remain alone or grouped in small units. Results obtained in the Camargue show that single subadults would soon attempt to find companions.

After a postpartum seclusion period (KURZ and MARCHINTON 1972; MAUGET 1980; SINGER et al. 1981), piglets leave the farrowing nest and follow their mother. The family group, comprised of the sow with its piglets, may thereafter grow larger by association with other animals as has been observed by SNETHLAGE (1957), GUNDLACH (1968), MAUGET (1980) or in the present study. Our results show that sounders – which result from the joining up of at least two family groups – are chronologically the first type of association. The good synchronization of births observed in the Camargue would facilitate their formation since piglets are of similar age and development. In other areas, sounders have been observed to form during the first two weeks after birth (SNETHLAGE 1957; MEYNHARDT 1982).

Sounders are the equivalent of nursery groups reported in other species of Ungulates such as caribou (PRUITT 1960), bighorn sheep (GEIST 1971) or reindeer (HELLE 1981). However, these groups seem to be smaller in wild pigs, although large sounder associations have sometimes has been observed by several authors (SNETHLAGE 1957; MEYNHARDT 1982; other references in SINGER and ACKERMAN 1981).

Extended family groups are formed from May through June. As observed in bighorn sheep (GEIST 1971), it seems that reassociations with yearlings occur only 3-4 weeks after young are born. For SNETHLAGE (1957), the spring separation from the mother is definitive. If some yearlings rejoin sounders in August, i.e. 4-5 months after births, most of them remain together and form large subadult-groups ("companies"). For his part, MEYNHARDT (1982) observed that the animals of the same matriarchal unit regroup only a few days after farrowing. In this case, the separation of group members is both more limited (see above) and more temporary than observed in the Camargue.